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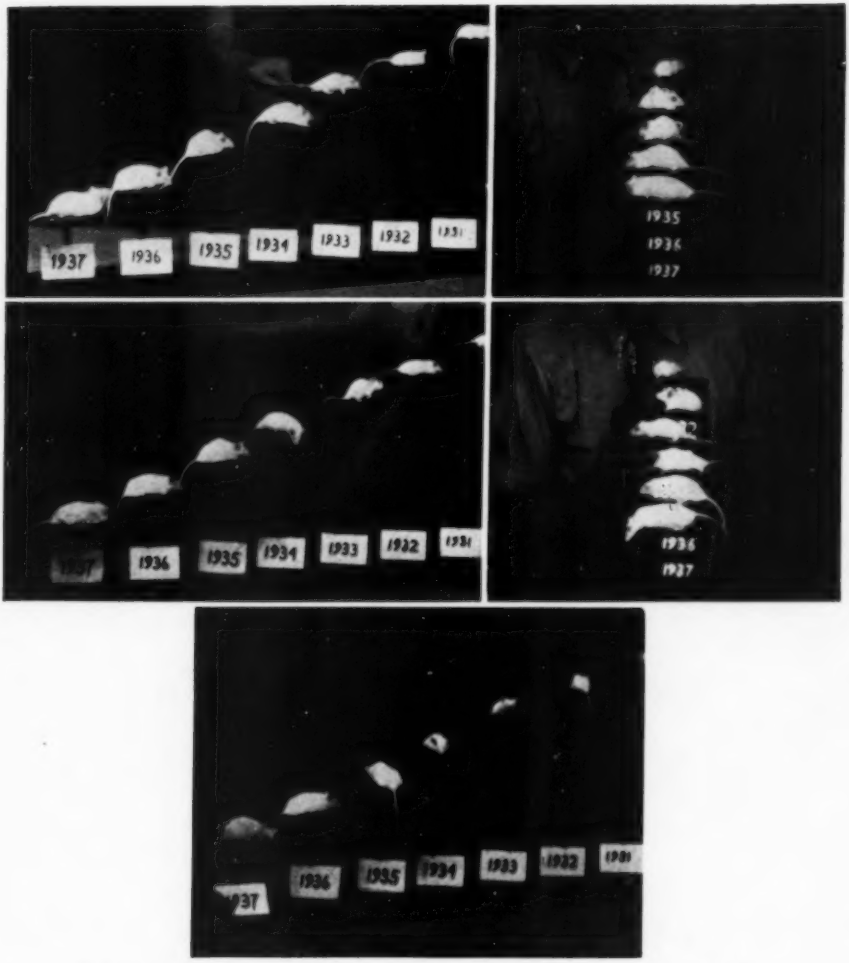
The Journal of HEREDITY



FROM MICE TOWARD "RATS" BY PROGENY SELECTION
(SEE PAGE 101)

Baltic Eugenics • The "Frayed" Fowl • Twins

VOLUME 29 MARCH, 1938 NUMBER 3

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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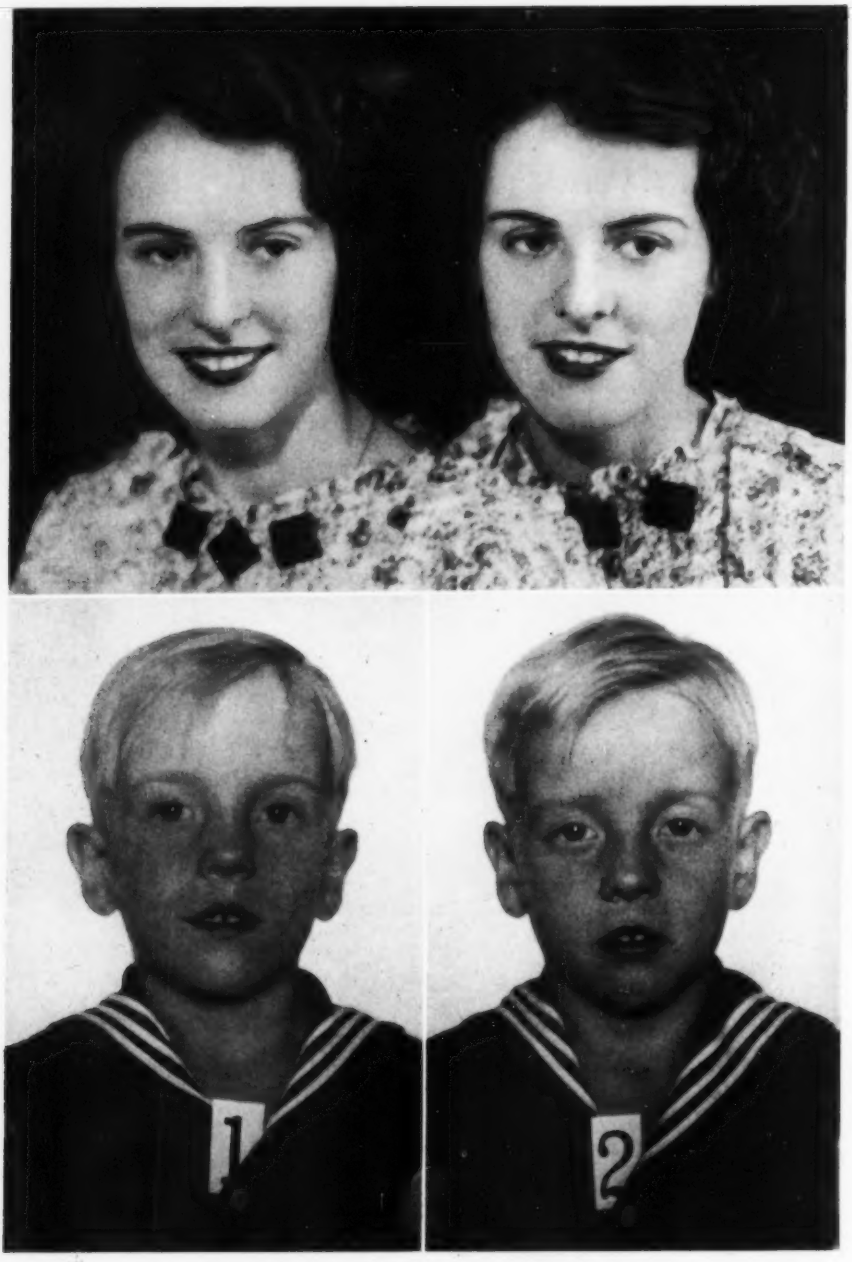


IDENTICAL EXCEPT IN TASTE ACUITY

Frontispiece

Misses Mary and Martha Johnson, of Mitchell, Ind. (Case No. 12), and Donald (1) and Roland (2) Brown, of Fort Wayne, Ind. Both of these pairs of twins are almost certainly identical, on the basis of all criteria employed, yet these twins are discordant with respect to ability to taste P.T.C. Donald and Martha are "Tasters"; Mary and Roland are not. Eye color, fingerprint patterns, blood groups, and other characteristics thus prove to be more reliable criteria taste acuity.

CONTRIBUTIONS OF THE 1937 NATIONAL TWINS' CONVENTION TO RESEARCH*

D. C. RIFE†
Department of Zoology, Ohio State University

IDENTICAL—?
Figure 1

Rita (left) and Renee (right) Hettler, of North Hampton, Iowa. (Case No. 8.) At Fort Wayne the author diagnosed these twins as identical, but later information from their mother indicates that they are fraternal. At birth the placentae were separate, and as babies Rita had lighter hair and eyes than Renee. Rita is right-handed and Renee is left-handed. They were Cesarean babies. Note in Table I that the three comparisons of their dermatoglyphics gave very similar results.

DIFFER MOST IN FINGERPRINTS
Figure 2

Misses Iris (left) and Agnes (right) Prather, of Grahn, Ky. (Case No. 46.) A pair of almost certainly identical twins, classed as fraternal on the basis of dermatoglyphics alone. Iris is right-handed and Agnes left-handed. MacArthur suggested, on the basis of greater heterolateral similarities, that these girls might possibly be identical, with reversal in handedness. The above photograph was taken from separate snapshots of each girl, which accounts for discrepancies in clearness and size.

ON August 28 and 29, 1937, the Sixth Annual Convention of the National Twins' Association was held in Fort Wayne, Ind. This unique Association was organized in 1931, and today has a membership of over 2,800 pairs of twins. Non-commercial in nature, the organization aims to enroll

*Funds for this research were procured through a grant from the Ohio Academy of Science.

†Genetic Studies of Monozygotic Twins, No. V.

as many as possible of the 2,000,000 twins in the United States in its membership. This year an attendance of more than 2,500 pairs of twins at the Convention was reported.

Saturday, the 28th, was registration day. In the afternoon there was a street parade of twins, and in the evening a banquet was held, twin entertainers appearing on the program. On Sunday contests were held and prizes awarded to the most similar and the most dissimilar pairs of twins of each sex, both above and below twelve years of age, the oldest and youngest pairs, the pair who came the greatest distance, and to the family containing the largest number of pairs of twins. The youngest pair was six months of age, and the oldest pair 81 years of age. One member of the latter pair came from Los Angeles by air to attend the Convention. At least thirteen states were represented.

The 1938 Convention is scheduled to be held in Chicago, and it is believed the 1939 Convention will be held in New York City, at the time of the World's Fair.

Mr. W. F. Whitmore, of the Publicity Committee, extended a cordial invitation to the author to attend the Fort Wayne Convention, and also to bring assistants* along for collecting scientific data from the twins. The invitation was accepted, and the Convention officials and all of the twins contacted cooperated splendidly in the setting up of test apparatus and in the collection of data.

Twin Diagnosis

It was felt that data obtained at the Convention might afford an opportunity to estimate the efficiency of dermatoglyphics, as compared with various other criteria, in the diagnosis of twins. Twins who are so similar in general body build; features; pigmentation of eyes, hair and skin; voice and mannerisms as to be indistinguishable to individuals not well acquainted with them are usually considered to be monozygotic, that is, identical in hereditary makeup. A recent study[4] of twenty such pairs of twins showed, on the basis of intra-pair comparisons of four qualitative genetic traits, and four quantitative traits, that the chances of sib pairs being as similar as these twins, ranged from one chance in 2,500 for the least similar pair, to one chance in 400,000 for the most similar pair. The implication, not necessarily true, easily follows that one minus the above probabilities gives the odds that a given pair are monozygotic. However, as only eight out of all the traits showing variation in sibs are included in the comparisons, and as only two types of twins are known to exist in man, such errors undoubtedly greatly underestimate rather than overestimate, in the great majority of similar twins, the actual probabilities of a given pair being monozygotic. In these twenty pairs of twins, no intra-pair variations were found in blood group and M-N blood reaction, whereas approximately 61 per cent of sib pairs show intra-pair variation in one or both blood reactions.

It would, of course, be gratifying if a single infallible criterion, rather than the general similarity method, could be found for distinguishing the two types of twins. Intra-pair variation in sex, blood group, M-N reaction, general pigmentation, and wide differences in general body conformation or features, are each in themselves conclusive evidence of dizygosity or fraternity, but intra-pair similarity in each or even all of these traits may occur in dizygotic twins. Our most definite and clear cut genetic traits, the blood groups and the M-N reaction, show no intra-pair variation in approximately 39 per cent of sib and fraternal twin pairs in North American whites.[5] Interestingly enough, the more intangible a trait, the more

*Blood samples were collected, and later analyzed, by Dr. Harriett Hyman, of Ohio State University. Dr. J. M. Rife, of Muskingum College, Mr. Milton Parker, Mr. Joseph Simkin and Mr. C. E. Boye, of Ohio State University, assisted in the collection of various other data.

variation, as a rule, do we find in fraternal twins. For example, in twenty pairs of identical twins, no significant intra-pair variations were found in the shade and distribution of iris pigmentation[4] whereas, in fifty pairs of sibs, no pairs were found that did not show such intra-pair variation. Such a trait, however, is of a too subjective nature to be entirely satisfactory for diagnostic purposes.

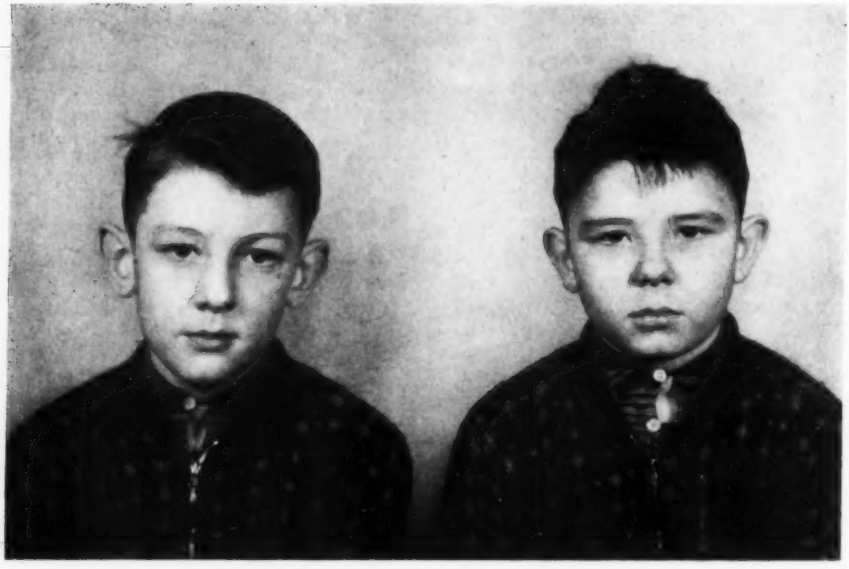
Aside from similarities in general appearance, dermatoglyphics have probably been used more frequently than any other criterion for diagnostic purposes. Like the blood groups, they are not subject to change after birth (except in size), they can be accurately recorded and definitely measured, and like more intangible traits, are capable of tremendous variation. Their chief weakness as diagnostic criteria lies in the fact that apparently they are subject to modification *in utero,* as each dermatoglyphic characteristic seems capable of intra-pair variation in expression in identical twins. As compared with intra-pair sib and fraternal twin differences, such variations are small, but at least up to the present time, have been sufficient to prevent the universal acceptance of dermatoglyphics as a sole basis of twin diagnosis.

It has been noted by various investigators that, in the majority of identical twins, the intra-pair similarities in finger and palmar dermatoglyphics are greater than the bilateral similarities of either individual. Based on comparisons of the finger and palmar dermatoglyphics of fifty pairs of assumedly monozygotic twins, fifty pairs of fraternal twins, sixty-two pairs of single sibs, sixty-five parent-child pairs, fifteen husband-wife pairs and one hundred and fifty random pairs, MacArthur, of Toronto University,[3] has recently devised an objective method for diagnosing twins, which promises to be of considerable value. This method, described in detail elsewhere,[3] consists of intra-pair and bilateral comparisons of finger ridge count values; finger patterns; main palm line terminations and axial triradii; and palm patterns. Diagnosis is based on the principle that in identical twins intra-pair similarities, either heterolateral or homolateral, usually the latter or both, are greater than the bilateral similarities of either individual, while in fraternal twins the situation is reversed.

Fort Wayne Data

The twins studied at the Fort Wayne Convention were first diagnosed by the author, on the basis of general similarity in distribution and shade of iris pigmentation, general pigmentation of skin and hair, and similarities in features, body proportions and mannerisms. Significant differences in any of these traits resulted in classification as fraternal. Only one pair of doubtful zygosity was encountered by the author, Case Number 8, shown in Figure 1. Although not similar to such a degree as to make them extremely hard to distinguish, no significant differences were found in the distribution of iris pigmentation, and certain other traits, which ordinarily vary in fraternal twins. As shown in Table I, they were first diagnosed as identical, but because of later information from the mother and the family physician (see Figure 1) the diagnosis has been reversed. Examinations of iris pigmentation were macroscopic, and in cases where zygosity was readily apparent from general appearance, were rather superficial. Blood samples were obtained from 46 pairs, and were later analyzed for group and M-N reaction. Fifty pairs were tested for P.T.C. reaction, and finger and palmar dermatoglyphics were obtained from 61 pairs. The prints were later given to Dr. MacArthur for analysis, whose diagnoses were based on the dermatoglyphics alone.

Table I summarizes the data. The twins are numbered in the order studied, and a few numbers are omitted, in cases where dermatoglyphics could not be obtained. Column 2 lists the sex of each pair, a total of 36 female, 18 male and 7 opposite sexed pairs. Results of the blood tests and taste reaction are



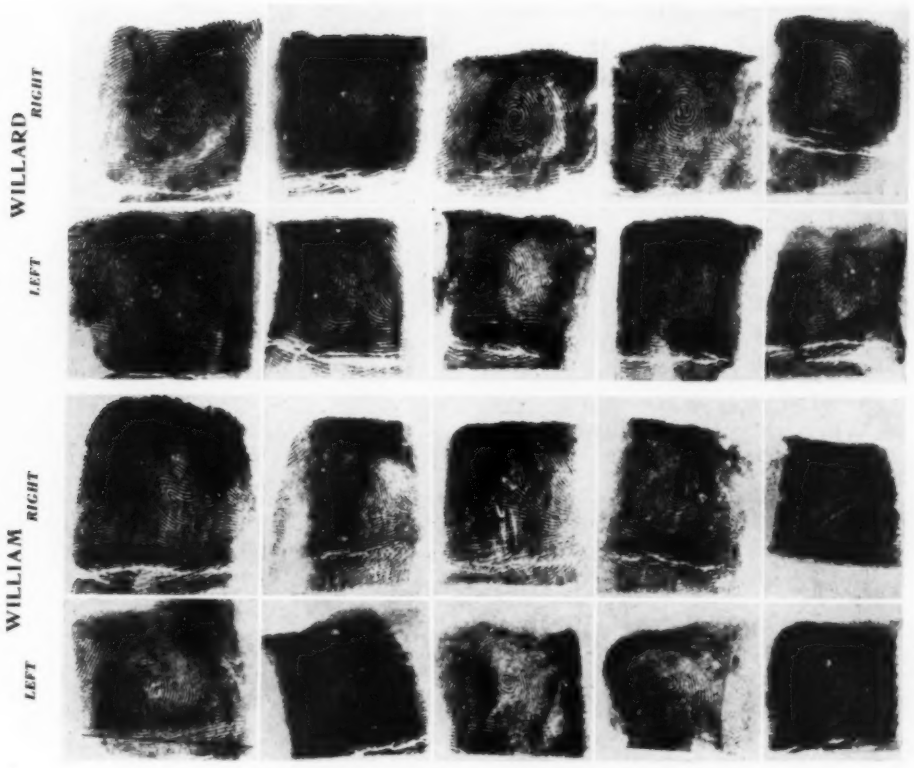
ALIKE ONLY IN FINGERPRINTS AND PALM PRINTS

Figure 3

Willard (left) and William (right) Scott, of Fort Wayne, Ind. (Case No. 29.) No further evidence is necessary to show that these boys are not identical. Willard has lighter hair and eyes than William and is different in a multitude of other ways. Yet their dermatoglyphics show greater cross-resemblance than right-left resemblance. (See Figures 4 and 5, also Table I.) They are seven years old, just one day younger than the girls shown in Figure 1.

next in order. A taster is designated by the symbol plus (+), and a non-taster by the symbol minus (—). In the next column, *A* signifies alike, and *U* unlike in distribution and shade of iris pigmentation. Rife's and MacArthur's diagnoses are next recorded, *I* signifying identical and *F* fraternal. The results of MacArthur's analysis of the dermatoglyphics are shown in the next three columns. The last column shows the handedness of 42 pairs of twins, *RR* denoting both members as being right-handed, *RL* one member as right-handed and the left-handed, and *LL* both as left-handed.

An examination of Table I shows that of the first twenty pairs examined, only two were fraternal. When this trend was observed, fraternal twins were at a premium, as we would have preferred approximately equal numbers of both types. At times the twins came in such large groups that it was impossible to obtain complete data on all pairs. In such instances, blood and taste tests of fraternal twins were preferably neglected, as wide differences in general physique and features, and differences in sex were in themselves conclusive evidence of dizygosity. The last fifteen pairs listed were not examined by the author, but were diagnosed by other members of the Ohio State group, following the same principles. None of the pairs classed as identical by either MacArthur or Rife showed intra-pair variation in either of the blood reactions. All of the pairs classed as identical by Rife were alike in iris pigmentation. Based on our knowledge of the modes of inheritance and on the frequencies of the genes involved in the two blood reac-

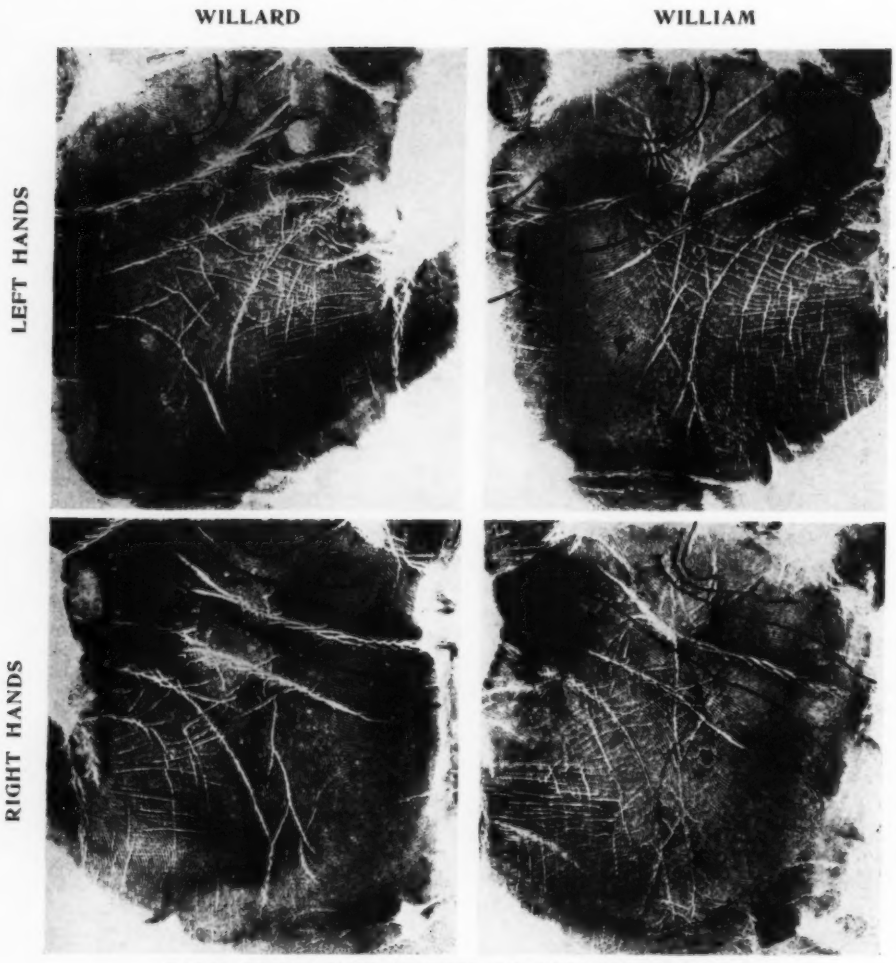


WILLARD-WILLIAM FINGERPRINT RESEMBLANCE

Figure 4

Note the presence of whorls on all of Willard's right fingers and on William's left fingers. This criss-cross resemblance in pattern is often found in identical twins.

tions and taste reaction to P.T.C., and also on our observations of the iris pigmentation of fifty pairs of sibs, we should expect fraternal twins to be alike in respect to all four traits in approximately one out of every 200 pairs. Sets Number 8 and Number 46 are the only pairs classed as fraternal by MacArthur, who are alike in respect to each of the above traits. The latter pair is shown in Figure 2 and is considered by Rife to be almost certainly monozygotic. We have previously discussed pair Number 8. The photographs of pair Number 29, classed as identical by MacArthur and as fraternal by Rife are shown in Figure 3, and their finger and palm prints are shown in Figure 4 and Figure 5. Pair Number 49, also classed by MacArthur, on the basis of dermatoglyphics alone, as identical, were likewise diagnosed as fraternal by Rife, because of striking differences in general appearance. Unfortunately, we have been unable to obtain pictures of this pair. Apparently, MacArthur's diagnosis, based on dermatoglyphics alone, was correct in 58 out of 61 instances, approximately 95 per cent. It would have been desirable to have had a higher proportion of like-sexed fraternals in the group, as unlike-sexed twins are easily diagnosed, but as fraternal twins were considerably in the



PALM PRINT SIMILARITIES OF WILLARD-WILLIAM

Figure 5

The inter-twin (homolateral) resemblances in the palm patterns are greater than the resemblance in patterns between the palms of either twin. This has been advanced as an excellent criterion of identity but in this case the rule does not hold for William and Willard (see Figure 3) are obviously not identical twins. (Such similarities in fraternal twins, however, are exceptional.) Where adequate data regarding a pair of twins are available, a combination of the best methods of differentiation would leave only a very few cases in which doubt would remain as to classification.

minority at Fort Wayne, all available pairs, regardless of sex, were included. Assuming pair Number 8 to be fraternal, of the 61 pairs studied, 37 pairs are almost certainly monozygotic, and 24 pairs dizygotic, seven of the latter being of the opposite sex. Even so, the fact that MacArthur's method is highly efficient is demonstrated beyond reasonable doubt, and, when one cannot actu-

ally see a pair of twins or their photographs, it would seem to be, with the possible exception of foetal membranes, the most valuable means for determining twin zygosity. Apparently several independent genetic factors play a part in the formation of finger and palmar dermatoglyphics. When dermatoglyphics of sibs and parents are also available for comparison with those of a given pair of twins, they are of great comparative significance in diagnosis, as demonstrated in the comparisons of the dermatoglyphics of the quints with those of three sibs.[2]

Taste Acuity

Reference to Table I reveals that three pairs of twins classed as identical both by MacArthur and Rife (Cases 3, 12, and 15) showed intra-pair variation in taste reaction to P.T.C. In the twenty cases of identical twins studied by Rife,[4] one pair was encountered showing intra-pair discrepancy in taste, yet diagnostic tests revealed that only once in 2,500 times should we expect sibs or fraternal twins to be so similar in respect to the other traits studied. The non-taster was later shown to have a general taste deficiency, which was thought to possibly be due to the non-taster's having had a severe case of poliomyelitis several years previously. In 1937, Ardashnikov[1] reported three pairs of almost certainly identical twins, out of a total of 137 pairs of identicals, who showed intra-pair variations in taste reaction to P.T.C. Thus in a total of 194 pairs of twins assumed to be identical by various criteria, seven pairs show discrepancies in taste of P.T.C. Of significance in this connection is the fact that all of the 194 pairs were tested for blood group, and 57 pairs for M-N reaction, and in no instance were intra-pair differences encountered. Whatever may be the cause of occasional intra-pair variation in identical twins in taste reaction to P.T.C., such variation alone seems of doubtful validity as a criterion of dizygosity.

TABLE I.

Case No.	Sex	Blood		P.T.C	Diagnosis			Percentage difference in dermatoglyphic comparisons			Handedness
		Group	M & N		Iris Pigmentation	Sibs	MacArthur	Bilateral	Unilateral	Interbilateral	
1	♀♀	O O		+ +	A	I	I	10.68	14.0	20.1	R L
2	♂♂	O O	M M	- -	A	I	I	35.6	36.1	34.35	R L
3	♀♀	O O	M M	+ -	A	I	I	25.4	12.6	25.4	R L
4	♂♂				A	I	I	30.5	10.3	27.6	R R
5	♂♂	O O	M M	+ +	A	I	I	36.1	24.75	32.0	R R
6	♂♂				U	P	P	15.0	43.0	43.0	R R
7	♀♀	A A	M M	- -	A	I	I	40.3	44.05	36.65	R R
8	♀♀	O O	M M	+ +	A	In	P	28.5	30.6	29.82	R L
9	♀♀	A A	M M	+ +	A	I	I	23.3	22.0	27.5	R R
10	♂♂	A A	M M	+ +	A	I	I	27.0	22.68	27.0	R R
11	♂♂	O O	M M	- -	A	I	In	25.1	27.5	30.0	R R
12	♀♀	O O	M M	+ -	A	I	I	20.0	8.58	14.72	R R
13	♀♀	O O	M M	+ +	A	I	I	21.15	16.0	23.65	R L
14	♀♀	A A	M M	+ +	A	I	I	29.6	14.35	30.65	R R
15	♀♀	A A	M M	+ +	A	I	I	25.5	22.5	29.06	R R
17	♀♀	A A	M M	+ +	A	I	I	23.25	21.05	34.05	R R
18	♀♀	O O	M M	+ +	A	I	I	25.9	14.9	18.1	L L
19	♀♀	O O	M M	+ +	A	I	I	31.25	28.0	32.25	R R
20	♀♀	O O	M M	+ +	A	I	I	17.45	17.45	19.45	R R
21	♂♂	A A	M M	- -	U	P	P	29.6	26.45	29.6	R R
22	♂♂			+ -	U	P	P	37.0	41.65	47.0	R R
23	♀♀	A A	M M	+ +	A	I	I	46.0	14.42	45.25	R L
24	♀♀	O O	M M	+ -	U	P	P	41.15	46.25	41.25	R R
25	♀♀	A A	M M	+ +	A	I	I	16.0	9.2	17.25	L L
26	♀♀	B B	M M	+ +	U	P	P	31.50	43.25	47.0	R L
27	♀♀	A A	M M	+ +	A	I	I	30.35	12.0	30.35	R R
28	♂♂				U	P	P	25.00	24.85	37.6	R R
29	♂♂	B O	M M	+ +	U	P	In	27.0	28.35	41.0	R L
30	♀♀	B O	M M	+ +	A	I	I	10.1	10.9	14.65	R R
31	♀♀	O O	M M	+ +	A	I	I	27.7	24.5	32.25	R R
32	♀♀	A A	M M	+ +	A	I	I	32.0	18.4	24.65	R R
34	♂♂	AB AB	M M	+ +	U	P	P	20.00	24.50	23.85	R R
35	♂♂				U	P	P	29.0	32.5	27.5	
36	♂♂				U	P	P	21.45	24.85	40.5	
38	♀♀	A A	M M	+ +	U	P	P	20.5	40.45	40.45	R L
39	♂♂				U	P	P	36.45	48.65	46.15	R R
40	♂♂				U	P	P	37.0	41.35	34.65	
41	♀♀	O O	M M	+ +	A	I	P	18.0	9.05	14.35	R L
42	♂♂				U	P	P	29.65	45.45	44.15	
44	♀♀	A A	M M	+ +	A	I	I	28.1	20.1	22.7	R R
45	♀♀	O O	M M	+ +	A	I	I	23.75	15.0	22.6	R L
46	♀♀	O O	M M	+ +	A	I	In	26.0	24.85	24.85	R L
47	♂♂			- -	A	I	I	26.75	11.05	26.75	R R
48	♂♂	A A	M M	+ +	U	P	P	24.85	20.04	21.65	R R
49	♂♂				U	P	P	23.65	17.4	20.4	L L
50	♀♀	O O	M M	+ +	A	I	In	22.4	13.85	23.05	R L
51	♂♂	O A	M M	+ +	U	P	In	19.5	14.05	13.05	
52	♂♂	O A	M M	+ +	U	P	P	19.8	28.25	21.05	
53	♀♀	A A	M M	+ +	U	P	P	28.1	24.4	40.2	
54	♂♂	O O	M M	+ +	U	P	P	16.25	40.25	40.25	
55	♂♂	O O	M M	+ +	U	P	P	24.15	15.95	24.5	
56	♂♂	O B	M M	+ +	U	P	P	20.25	19.7	28.95	
57	♂♂	O B	M M	+ +	U	P	P	17.2	49.25	49.25	
58	♀♀	B B	M M	+ +	A	I	I	28.25	29.25	23.65	
61	♂♂	A AB	M M	+ +	U	P	P	28.7	40.75	42.0	
62	♂♂	A A	M M	+ +	U	P	P	28.25	32.72	29.25	
63	♂♂			+ +	U	P	P	29.4	44.25	42.0	
64	♂♂				A	I	I	20.75	19.61	28.25	
66	♀♀	O O	M M	+ +	A	I	I	24.75	16.45	26.6	
67	♂♂	O O	M M	+ +	A	I	In	20.2	20.75	25.2	
70	♂♂				A	I	I	25.0	16.75	40.6	

*See Fig. 1.
†Diagnosis not considered certain by MacArthur.

The data taken at Fort Wayne is confirmatory of previous studies, in indicating that twins who are so similar

Forty-two pairs were tested for handedness in unimanual operations, thirty-one pairs being identical and eleven pairs fraternal. Table I reveals that nine of the identical pairs (29.0%) and three of the fraternal pairs (27.2%) show reversal of handedness within the pair. Of the three pairs in which both members are left-handed, two are identical and one fraternal. These data do not support the belief, held by many, that reversal in handedness or "mirror-imaging" occurs with much greater frequency in identical than in fraternal twins. Data on handedness is apparently of no value whatsoever in twin diagnosis.

Conclusions

in general appearance as to be easily mistaken for one another, are, in the vast majority of cases, identical or monozygotic. In identical twins the distribution and shade of iris pigmentation, as a rule, shows no significant intra-pair variations, whereas the reverse is true for fraternal twins. If one cannot actually see a pair of twins or their photographs, dermatoglyphics can be relied upon as diagnostic criteria, in a high percentage of cases. In cases of doubtful zygosity, blood groups and M-N reaction are of value, in that intra-pair variation in either is conclusive evidence of dizygosity. Taste reaction to P.T.C. is of doubtful value in twin diagnosis, except when used in conjunction with other independent traits, and in setting up formulae predicting the frequencies that sibs as similar as a given pair of twins would be expected to occur. The efficiency of the above criteria are increased if similar data from sibs and parents are also available.

The writer wishes to thank those who assisted in the collection of data, also Dr. J. W. MacArthur for his analysis of the dermatoglyphics, and the twins for their patience and cooperation in submitting to various tests.

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An Artificial Sex-Linked Character

THE event of the biennium has been the translocation by X-raying of a section of chromosome in the grouse locust carrying the gene *W*, for a stripe along the femora of the posterior legs, and attaching it to the sex, or X-chromosome. We thus now have a sex-linked character, the first to have been reported in any of the orthoptera. The deficient, or donor, chromosome was lost in the matings which followed, but the accreted, or receptor, chromosome was retained and has been carried through eight or ten generations, and in rather large numbers. The translocation marks a very profound change in the inheritance of these grouse locusts. The characteristic (stripes along the legs) is still carried in its original position and inherited in the regular way of autosomal characteristics. At the same time the identical characteristic is, even in the same individual, inherited in an entirely different (sex-linked) way. This one is different from most sex-linked characters previously reported in other animals in that it is a dominant and the females show a single dose as well as the males.

Another peculiarity about this new sex-linked characteristic is that females carrying it double, or on both sex chromosomes, apparently do not hatch, or at least do not grow up to be recorded. We assume that the translocation consisted in an addition of chromatin to the sex-chromosomes above the normal, and that there is too much of it, or whatever it bears, when both X-chromosomes have it.—*Biennial Report of Kansas Experiment Station.*

A HERITABLE VARIATION OF FEATHER STRUCTURE IN THE FOWL*

D. C. WARREN
Kansas State College

FRAYED WING FEATHERS

Figure 6

A female showing the expression of the recessive character, fray in the tail and wing feathers.

THIS variation in feather structure was brought to the writer's attention in 1931 by John DeForest, a poultry flock inspector in Kansas. It appeared in a flock of the Ancona breed and had been observed there for a number of years.

This new factor is characterized by a frayed appearance of the flight and tail feathers. There is considerable variation in expression of the character and in extreme cases the body feathers are lacking in smoothness and have a slightly ropy appearance. However, in

*Contribution No. 109, Department of Poultry Husbandry.

DEFECTIVE BARBULES

Figure 7

Flight feathers from frayed and normal plumaged birds.

most instances the condition is noted only in the tail and wing feathers. When the wings are folded normally, the frayed condition will be observed in the tail feathers only.

This factor has been designated as "fray" and the symbol *fr* is proposed. This character is not recognizable at hatching, and is somewhat difficult to detect in the first set of chick feathers, especially in individuals showing less extreme expression of the factor. The second and mature set of feathers show the fray character much more definitely. The molt of the original wing feathers begins at about 6 to 12 weeks of age, depending upon the maturity age of the bird. As the bird grows an increasing number of new wing feathers, the frayed condition is more easily recognized.

In chicks which feather out early, fray may be recognized with a high degree of accuracy in chicks about a week old. Although the fraying is somewhat obscured as the feather matures, it is rather easily recognized during the first few days after the feather emerges from its sheath.

Birds showing this character seem to be lacking in viability, but this may be a result of the inbreeding usually necessitated in the study of a recessive factor, rather than being due to the effects of the factor itself.

Microscopic examination of flight feathers of frayed birds shows that the frayed appearance is due to a defective condition of the barbules. This is particularly true of the anterior barbules and hooklets. Some hooklets are present but they are usually more sparsely distributed on the shortened and frequently misshapen barbules. This defective feather structure usually results in an imperfect interlocking of the anterior and posterior barbules. The separated barbs give the frayed appearance of the vane.

Two frayed females were secured originally and from them the stock became established. The results of the various types of crosses are given in Table 1. The F_1 generation was produced by crossing frayed individuals to different types of crossbred birds carried at the Kansas State College poultry plant. These crossbreds usually carried other dominant characters which were useful in testing linkage relations of this new factor. The results of linkage tests are to be reported elsewhere.

The results of matings reported in Table 1 indicate that fray is a simple autosomal recessive. There is considerable shortage of the segregating frays, but this may be due to the effects of the character in lowering viability of the chicks. Also in the earlier matings it is probable that some of the birds showing fray in the less extreme condition were overlooked.

Table 1. Results of matings of the character, fray

	Daughters		Sons		Total	
	Fray	Normal	Fray	Normal	Fray	Normal
Fray ♂ × Normal ♀		138		147		285
Normal ♂ × Fray ♀		116		117		233
F_1 ♂ × Fray ♀	503	772	669	947	1172	1719
F_1 ♀ × Fray ♂	589	638	668	756	1257	1394

◆

Discovery of Hairless Goat

SIR:

With reference to my recent article in your Journal on the hairless goat (vol. 28: pp. 265-266, 1937), I wish to note a correction regarding the discovery of this interesting mutation. Through my fault the discovery of the hairless goat was ascribed to Mr. Trifonov, whereas it had been first discovered by Professor M. S. Karpov. The matings described in my article were made by Mr. Trifonov under the guidance of Professor Karpov, to whom should be given credit for the discovery. I regret this unfortunate error.

D. A. KISLOVSKY

FLOWERING HABIT CONTROLLED BY DAY LENGTH

Figure 8

Annual sugar beets are biennial in short days: *A*, cool short; *B*, cool long; *C*, warm short; *D*, warm long. In this species—or at least in the variety under study—length of day and not temperature was the deciding factor, in contrast to the situation illustrated in Figures 9 and 12.

PHOTOPERIOD, TEMPERATURE AND SOME HEREDITARY RESPONSES OF PLANTS*

R. H. Roberts and Burdean E. Struckmeyer
University of Wisconsin

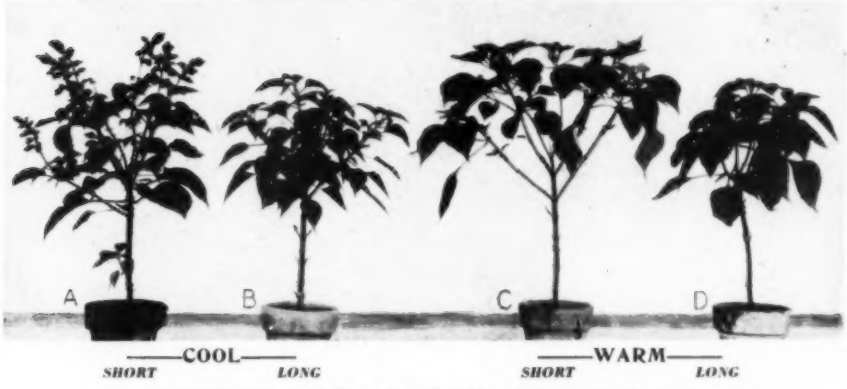

Figure 9

Temperature modifies the photoperiod responses of some plants as Salvia: *A*, cool short; *B*, cool long; *C*, warm short; *D*, warm long. In contrast to the situation in the beet (Figure 8) the short-day reaction of Salvia is affected by the temperature, the cool short day producing precocious flowering.

IN connection with a study of the relation of phloem development to blossoming[2] more than 120 species and varieties of plants were grown in different temperature and photoperiod environments to secure samples for anatomical observation. Long- and short-day conditions were provided in two greenhouses carried at minimum temperatures of 55° and 70° F., furnishing four environments. From the physiological point of view an outstanding result of the tests was that temperature effects modified or altered the length of day responses of many kinds including such so-called specifically photoperiodic plants as poinsettia, *Rudbeckia*, *Cosmos*, soybean, *Salvia* (Figure 9) and Maryland Mammoth tobacco.[3, 4]

From the standpoint of heredity there were a number of interesting results. Three cases will be reviewed.

Klondyke Cosmos is a typical "short-day" plant and fails to blossom in northern latitudes before it is killed by fall frost. A sport of this variety appeared in 1934.† This new variety, which has been named Orange Flare, blossoms in July. It was assumed to be a photoperiod variant. Experiments proved otherwise. When growing in a cool temperature, Orange Flare is a short-day plant but in a warm temperature it blossoms in long days as well as short days. The variation from

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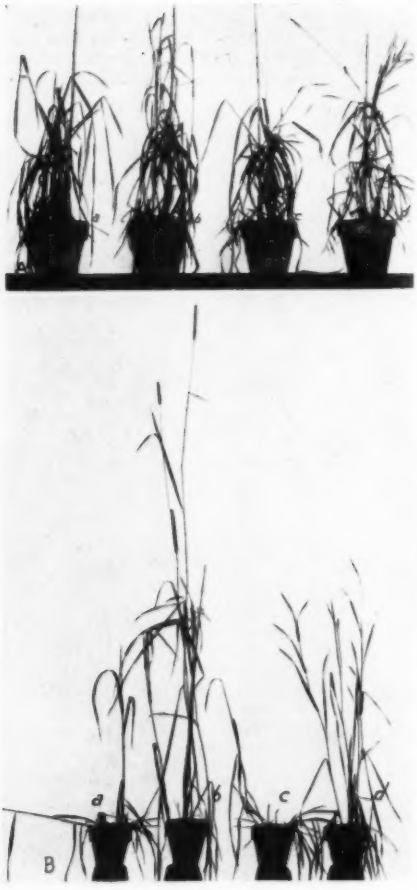
†Correspondence, Miss Elizabeth Bodger, El Monte, Calif.



VARIETAL DIFFERENCES IN REACTION

Figure 10

Great differences in reaction to temperature and length of day are shown by these timothy varieties. Variety *A* grows at about the same rate under all of the four experimental environments. Variety *B* requires a cool long day to progress to the heading stage.

DIFFERENCE IN OAT VARIETIES

Figure 11 (at right)

Responses of winter (*A*) and Wisconsin No. 7 oats (*B*): *a*, cool short; *b*, cool long; *c*, warm short; *d*, warm long. The winter oats respond to day-length alone, whereas the other variety (*B*) seems to require both temperature and day-length optima to head.

HIGH TEMPERATURE FLOWERING

Figure 12

Orange Flare Cosmos, a sport of the "short-day" Klondyke variety (which ordinarily does not blossom until fall), blossoms in the summertime because of high temperatures. *A*, cool short; *B*, cool long (vegetative phase); *C*, warm short; *D*, warm long (flowering). The parent form of cosmos blossoms ordinarily only in short days, regardless of temperature. Thus the mutation represents a change of reaction to temperature rather than to length of day.

POTATO INDIVIDUALISM

Figure 13

Potato varieties react differently to similar treatments: *A*, Triumph; *B*, Irish Cobbler; *a*, cool short; *b*, cool long; *c*, medium temperature, normal winter day; *d*, warm short; *e*, warm long. In genetic experimentation and in practical breeding programs such differences as these emphasize the need to control both length of day and temperature in reaching conclusions regarding growth habits.

Klondyke is obviously for temperature and not length of day.

In the course of a study of bolting of sugar beets by investigators from the United States Department of Agriculture annual strains have been selected.[1] Number 2240 blossomed in long days of both cool and warm temperatures (Figure 8). It also failed to blossom in short days at both ranges of temperature. Temperature would thus appear to be less of a factor in seed stock production of sugar beets during the first growing season than is photoperiod.

Another result of the temperature and photoperiod treatments was the clear demonstration that some varieties of a single species show a wide adaptation to the environments used whereas others thrive in only a single situation. Examples of plants showing this variability were timothy (Figure 10), oats (Figure 11), and potato (Figure 13). From the differences in reaction which these and other plants gave, the question arises as to whether adaptation to ranges of temperatures, light or other factors should not be more carefully

measured and the resulting information employed to a greater extent than is now done in the breeding of agricultural and horticultural plants.

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◆

A CLASSIFICATION OF SPLIT PERSONALITIES

ALTHOUGH Kraepelin's classification of dementia precox types and Bleuler's concepts of schizophrenia are still definitely in the foreground in psychiatric thinking, the tendency to consider "schizophrenia" as representing a variety of different forms of mental disease is rapidly gaining ground. Kleist's more recent classification of these disorders includes a number of undifferentiated forms. Moreover, he has classed the "degenerative psychoses" or deterioration forms apart from the atypical schizophrenias.

The author of the present book* takes the final stages in schizophrenia as his points for orientation. He holds that any classification of diseases from manifestations in their early stages has the disadvantage of dealing with symptoms in the process of development, and with the possibilities of changes in the future due to new or repeated attacks of the disorder. The transitory forms of schizophrenic manifestations he classifies as subtypes, which, however, appear definite and clear cut in their clinical aspects. He separates the material as a whole into two main divisions, i.e., a biological or inherited group and a subvariety group, the distinction being made on the basis of the character of the clinical manifestations. As systematized "defect" types one finds (1) paranoid schizophrenia with phantasophrenia, hypochondriacal hallucinosis, and "verbal" hallucinosis listed as subtypes. The difference between the hallucinations of the hypochondriac and the patient having "verbal" hallucinations is outlined on the assumption that the hallucinatory experiences in the hypochondriac are in the form of distorted perceptions, while those of the verbal type are clear cut and in the sensory sphere only. The three forms may be difficult to differentiate in the acute stages of the disorders where the patient's mental confusion dominates the picture and where a mixture of symptoms may appear. However, the respective causes of these diseases indicate that they are not derived from one source but constitute independent forms. Other subtypes are expansive paranoid reactions, incoherent schizophrenic defect (severe form), and autistic form, with the concepts of each founded on the study of a group of selected cases; (2) hebephrenia, with "nonsense" and eccentric forms as subtypes; and (3) catatonia with inert and active speech types, negativistic and rigid reactions mentioned among the subvarieties.

The various symptoms are expressed in distinct combinations in these subtypes and in a manner to indicate that they represent different diseases or independent syndromes. The investigation of families strongly suggests an hereditary basis for these forms.

The other schizophrenic forms are represented by stuporous reactions, pe-

*Leonard, K. Die Defektschizophrenen Krankheitsbilder (Ihre Einteilung in Zwei Klinisch und Erbiologisch Verschiedene Gruppen und in Unterformen Vom Charakter der Systemkrankheiten). Pp. 134. Georg Thieme, Leipzig, 1936.

riodic schizophrenia and schizophasia. These atypical varieties are not further divisible into subforms and are not identified with the other expressions of schizophrenia, but express a characteristic symptomatology, follow a particular course and probably have special hereditary factors. The author's special divisions of the schizophrenia problem are unusual and are based on what some may consider the "secondary" rather than the "primary" characteristics and manifestations of the disorders. However, new viewpoints and attempts to classify thinking should be welcome in a field where so many complex issues are at present under consideration and investigation. The material as presented suggests a number of additional problems worth studying in more detail.

N. D. C. Lewis
New York State Psychiatric Institute and Hospital

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BALTIC EUGENICS

EUGENICS in the three Baltic countries, Estonia, Latvia and Lithuania, is reported in a new publication *Iuventute Baltica*. It is the organ of the Children and Mothers Protection Committee of the Baltic States and is edited by Dr. H. Madisson, Tartu, Estonia. Most of the articles have summaries in English or German.

The first issue indicates an active interest in the subject of eugenics in this region. The broad outlook of the committee includes many items which would be classed as of secondary eugenic importance, though the need to carry on eugenic reform in the frame of existing social agencies makes such a classification somewhat arbitrary.

The concluding issue of the first volume contains a most interesting account of the Estonian sterilization law which was adopted only this year. The following statement by Dr. Madison summarizes the history of the law. The full text of the law (in German) is given following this discussion, but this is not reproduced here.

The Estonian Sterilization Law*

H. Madisson

On the 1st of April, 1937, the law of sterilization, decreed by the President on November 27, 1936, became effective. Thus the continuous struggle of Estonian doctors, which lasted over a number of years, was ended. People who were hereditarily defective could now be sterilized, though restrictions were still numerous.

Already in 1924 at the Estonian Medical Congress, eugenic problems had been discussed and a commission was chosen to formulate the principles of this law. In 1925 the fourth Estonian Medical Congress adopted these principles. The author of these lines introduced in 1925 the project of the sterilization law (Tulev Essti, 1925, No. 7, 8 and 9). Meanwhile the project of a new penal code had almost been worked out. In order to prevent the prohibition of sterilization by this code the author submitted in 1927 a paragraph to the Eugenic Commission, who in turn brought it to the attention of the Legislative Penal Commission. To begin with the latter rejected it. Subsequently the Estonian Medical Congress repeatedly urged the introduction of eugenic sterilization, but in vain. In 1934 the Estonian Eugenic and Genealogic Society submitted the law of sterilization to the government. This law was drawn up by the author. Eugenic abortion was included in this project. The second National Educational Congress voted in favor of a sterilization law. Due to these continuous requests the administration of the Public Health Assistance presented to the government a project of the steriliza-

*Translated by Irene Myer.

tion law, and finally, after many difficulties, the law of sterilization was introduced.

Since the Estonian sterilization law is the youngest amongst its equals it ought to have utilized more courageously the wealth of experiences accumulated in Scandinavia and Germany.

On the basis of §1 sterilization or abortion are only permitted in the case of hereditary lunatics, feeble-minded, people afflicted with serious hereditary epilepsy, and people with inherited incurable physical defects. Thus in each individual case of schizophrenia and lunacy its heritable nature must be proved. The permission to sterilize delinquents and drunkards comprised in the Scandinavian, Finnish, and German law is not included in the Estonian law, though these hereditary ills are more dangerous than the procreation of a child suffering from a physical defect.

A deplorable omission in the law is the fact that it has made no provision for the abortion of a woman rendered pregnant by a lunatic. Sterilization and abortion on social grounds are not permitted.

The sentence of sterilization is imposed by two district commissions one at Tallin and one at Tartu. Estonia is divided into these two districts, approximately there are 600,000 inhabitants in each. (§4.)

A district commission according to the law is composed of five people, the president must be a doctor of the town in which the commission resides. The Administration of Public Hygiene and Assistance appoints two medical specialists, a fourth member is nominated by the town municipality where the commission resides and a fifth member is nominated by the communal rural administration of the same town. It is not obligatory for the two latter members to be doctors, but for the present they are. Pracice has shown, that a commission of five is unnecessarily numerous, in particular as under adverse circumstances two of the five members might be laymen, not well versed in medical and eugenic questions (§4). The duty of the commission is to question experts and witnesses and to reach a resolution regarding sterilization or abortion (§).

The resolution of the commission is confirmed or refused by the director of the Administration of Hygiene and Public Assistance. The third and supreme instance of appelation is the Supreme Tribunal (the State Tribunal) in which no doctor participates (§8 & 9). The reasons for abortion must be decided upon within a month at the latest (§9). The work of the Commission is regulated according to the order of administrative procedure. A request for sterilization or abortion can be presented: 1, by the person desiring the operation; 2, by two official doctors; 3, by guardians, curators or protectors of people irresponsible for their actions, provided they are not heirs of the person to be sterilized; 4, by directors of institutitons of the Public Assistance and by directors of clinics and hospitals. We regret that close relatives of a deficient person are not granted the privilege to request an abortion or sterilization, because after all the procreation of children inferior in value primarily affects them (§3).

Once the resolution has been passed sterilization or abortion must be performed in medical institutions designated for this purpose. The operation cannot be performed by doctors who are members of the commission or who had personally requested the operation (§11). At the latest seven days after the operation a report has to be made (§12). Expenses incurred are met by the state or by the person on whom the operation had been performed, provided that he had requested it and had the necessary means (§13).

The work of the Commission is confidential and never published (§15), everybody is strictly obliged to keep it secret. On the other hand the doctors questioned by the Commission are exempt from this duty and may reveal the medical secrets of the person involved. A definitely approved operation can be performed by force (§10). The operation, however, cannot be carried out if it endangers the life and health of the individual, or if the latter is under ten years of age (§2).

A STUDY OF THE INHERITANCE OF BODY WEIGHT IN THE ALBINO MOUSE BY SELECTION

H. D. GOODALE

Mount Hope Farm
Williamstown, Massachusetts

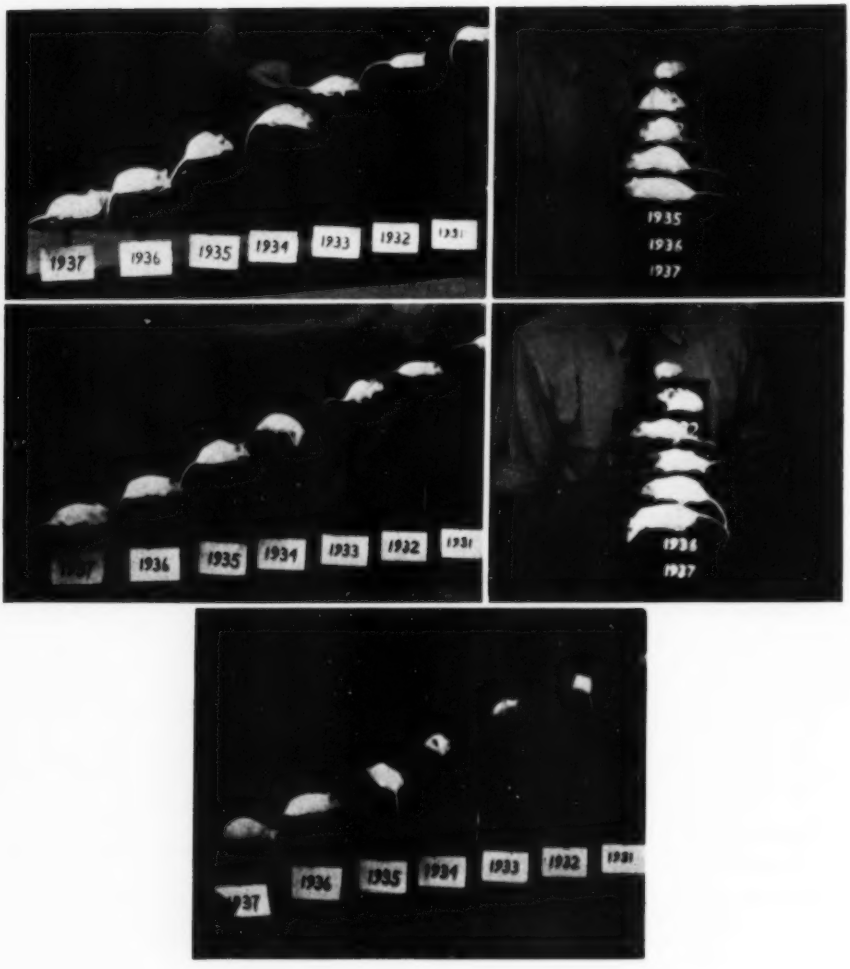
MANY experiments have been made on selection of breeding stock as a means of producing change in a species or race, but no experiment—so far as we have been able to learn—has ever been made which sought to learn the limits of change when the progeny-test method of selecting breeding stock is employed to produce change in characters which, in so far as they themselves are concerned, can undergo unlimited change. Yet our experience in the routine use of the progeny test at Mount Hope Farm, in the breeding of poultry for the improvement of characters having economic value, leads us to conclude that the progeny test, understood and used as it is understood and used at Mount Hope Farm, contains the possibility of producing an indefinite or even an unlimited amount of change in characters which themselves offer no obstacles to unlimited change. The truth of our conclusions can be demonstrated only by means of experiments. They might very well have been conducted with poultry, but the nature of our work with poultry makes their use inadvisable in the proposed experiments. However, the question of limits is much too important, both theoretically and practically, to be dismissed for this reason alone. We decided, therefore, to undertake some of the necessary experiments, using for this purpose an animal that could be bred easily in large numbers and characters which permit large or unlimited change. One of these experiments is reported here.

Mice possess many advantages for experiments of this kind, and weight is free from the objection that its very nature will bring the experiment to a quick conclusion. It is conceivable that mice might be developed by breeding which would weigh more than rats. Indeed, since the theory of evolution says that life began with a single-celled animal of no greater size than an amoeba, the very large animals such as mastodons, megatheria or titanotheres must have arisen from smaller ancestors.

We began, therefore, at Mount Hope, in 1930, an experiment which has as its object to breed mice as large as possible, and have already achieved results which demonstrate that the weight to which mice can be developed by selection cannot be predicted from a study of weight in existing strains. On the contrary, the present rate of progress is indicative of continued increase.

The chief object of this experiment is, as stated, so far as we can do so, to determine limits of change which can be made by selection and we plan to find these limits by breeding the largest and heaviest mice possible. The nature of the work is such, therefore, that information on the following related subjects will probably be obtained:

1. Comparison of the actual results, both of individual matings and of the entire series of matings, with the results expected on theoretical grounds, may supply further information on the genetic nature of weight inheritance.
2. Published reports on selection experiments usually lay no stress on genotypic selection, as compared with phenotypic selection. Indeed, in most cases, in so far as published statements are available from which to judge, genotypic selection, described—as applied in this experiment—on page 108, has not been used. The effectiveness of genotypic selection as a means of producing extensive genetic change is, therefore, being tested.
3. As any experiment on artificial selec-



SIX YEARS' PROGRESS IN PROGENY SELECTION

Figure 14

Enlarged moving-picture film views of mice showing increase in body weight obtained during the six years of the experiment. The five views show various positions of the mice, so that a composite idea of the visible increase in size can be gained, better than would be obtained from posed photographs. The 1931 foundation animals were large mice. Their descendants 12-16 generations later are thus definitely giants. Since no decrease in rate of gain has been noted in recent generations, there is an excellent possibility that by genotypic selection (i.e., by the selection of the parents to continue the strain through observing the weight of their progeny)—mice as large as rats can be produced in a relatively short time. The theoretical and practical implications (in animal breeding) of such a possibility are very great.

tion may add to our knowledge of natural selection, the present experiment may be favored in this respect.

4. If mice weighing twice as much as the ordinary laboratory mouse can be produced by selective breeding, it is reasonable to suppose that the productive ability of farm plants and animals can be improved to a like extent by genotypic selection, thus contributing to an increase in farm profits and improvement in farm life.

Maximum Weight and the Multiple Factor Theory

The second, third and fourth subjects require no further discussion at this point. However, the chief object of this experiment and its corollary, the genetic nature of weight inheritance, should be considered in relation to the one generally accepted explanation—the multiple factor theory—of the manner in which selection accomplishes the changes which occur under its action.

According to this explanation, the variation in size which supplies the material on which selection acts is the result of diverse combinations of genes. The changes which follow artificial selection are referred, therefore, to the accumulation of favorable genes which were present in, but dispersed among, the stock from which the foundation animals were taken, in such a manner that only mice of ordinary size are seen. Consequently, it is commonly concluded that when all favorable genes are assembled together in each individual of a strain, further change is impossible, except as those changes in genes, called gene mutations, occur. But the nature and frequency of gene mutations is such that, in the absence of positive evidence to the contrary, change due to favorable gene mutations is probably extremely slow, so slow that an experiment on selection—unless continued over impractically long periods of time—could not rely upon gene mutations to promote further change. In the absence of gene mutations, the limits beyond which selection is powerless to effect further change must be predetermined by those genes which were present in the foundation animals. It is important, then, to learn as much as possible about the amount of change in the weight of the mice of this experiment, which might be brought about by accumulating in all individuals of some future generation as many genes as possible which favor heavier animals, and by discarding as many as possible of those that favor smaller animals, because if an amount of change is produced by selection which exceeds the theoretical limits, a new explanation must be sought. Castle's[1, 2] discussion of blending inheritance in relation to the gene theory offers interesting possibilities in this direction.

Genes, in respect to weight, are of three kinds; neutral, plus and minus. Since neutral genes have no influence on weight, each chromosome can be regarded as a linear series of plus and minus genes which, according to the excess of one kind of gene over the other, becomes a plus or a minus chromosome. The twenty pairs of chromosomes of the mouse are, then, equivalent to twenty freely segregating pairs of weight genes. The effect of each chromosome on weight presumably differs from each of the others and presumably changes from time to time, because of cross-overs. As the chromosomes, unlike the genes in the chromosomes, are independent bodies, the first effects of selection may very well be the results of a rearrangement of chromosomes which, notwithstanding complications introduced by cross-overs, produces a race characterized by the presence of those chromosomes which favor increased weight.

Sorting of chromosomes is, however, only one phase of the problem. Since each chromosome is a linear series of plus and minus weight genes, selection, in order to reach a limit beyond which further accumulation of plus genes is impossible, must disentangle the plus genes from the minus genes in each chromosome in order that each chromosome of later generations may carry as complete a complement of plus genes as possible, having in mind that selection is effective only on loci represented by unlike alleles. The task of disentangling the plus genes from the minus genes may well extend the labors of the breeder for

an indefinite period before it is completed.

Of all the loci in a race or species represented by unlike alleles, only part may be available in an experiment on artificial selection. One reason for this is that the foundation stock frequently consists of only a few individuals. The number of loci represented by unlike alleles is, therefore, correspondingly reduced, particularly in the case of those loci where the frequency of one allele is small, relative to that of its companion, —or companions, if multiple alleles occupy the locus. Then, too, an experiment in artificial selection is necessarily limited by time, space and expense to very small numbers in comparison with those available in nature, a circumstance that apart from the effects of selection, tends, as the experiment proceeds, to reduce the number of suitable loci. Nevertheless, the number of suitable loci may be very large, much larger, indeed, than might be anticipated from a series of measurements made on members of the race, a series which contains only a small number of individuals compared with the numbers necessary to cover the entire range of genetic classes when more than a few pairs of heterozygous genes are concerned. Thus, ten pairs of heterozygous genes segregating independently of each other require 1,048,576 individuals to cover the range of genetic classes, while twenty pairs, which is only one pair of genes to each pair of chromosomes in the mouse, require 1,099,511,627,776 individuals. In view of these very large numbers which are, after all, small compared to the theoretical requirements when larger numbers of pairs of genes are concerned, the size of the sample of a population which is measured as a preliminary to a selection experiment, while statistically significant, is really insignificant and affords no indication of the number of genetic classes involved.

The problem of determining a theoretical limit beyond which selection ceases to be effective is a problem in mathematical genetics, beset with many complicating elements. In one sense no solution is possible, since the number and the effect of the genes concerned are not known, while dominance, multiple alleles, the influence of particular combinations of genes, heterozygosis, etc., all contribute complicating elements. Nevertheless, an estimate of the maximum amount of change under certain conditions is possible and is well worth considering in connection with the present experiment.

Estimating Maximum Weight

In making this estimate, advantage may be taken of the principle that the frequencies of the classes in a random sample drawn from a larger population are proportional to the frequencies of the classes constituting the larger population. Now, heterozygous non-dominant genes of equal effect and equal frequency are distributed in classes according to the expansion of the even powers of the binomial $(a + b)^n$. The number of genetic classes of different numerical values is, accordingly, $n + 1$ and the frequency of each class is given by the numerical value of the coefficient of each term in the expanded binomial. The number of pairs of genes is $\frac{n}{2}$, and the least number of individuals required to include all genetic classes is 2^n. When the number of pairs of genes is small, less than five or six, 1024 or 4096 individuals should include, theoretically at least, representatives of all genetic classes. But as the number of gene pairs increases, samples of a size that are available in a practical sense, say one thousand individuals, include representatives of a progressively smaller proportion of all genetic classes, due to the decrease in relative frequency of each genetic class from the center outwards, which soon reaches a value too small to be included in a sample of this size,* and so, with an increasing

* As a sample of one thousand individuals is a large sample, as samples of biological populations go, this number will be understood whenever the word "sample," without qualification, is mentioned in this discussion.

number of pairs of genes, a progressively larger proportion of all genetic classes is excluded from the sample. But these excluded classes provide the basis for corresponding increases in the amount of change which may be accomplished by selection. For example, when there are eight pairs of genes, there are seventeen genetic classes, of which thirteen should be included in the sample and four excluded. When there are eighteen pairs of genes, there are thirty-seven classes of which nineteen should be included in the sample and eighteen excluded. When there are twenty-five pairs of genes, twenty-three classes should be included in the sample and twenty-eight excluded from it. It follows, therefore, that a definite proportion of all the classes resulting from any number of pairs of genes is included in the sample, and that from this proportion the limits of selection for a particular number of pairs of genes may be determined.

The sample of which we have been speaking is an ideal sample, and its relation to the classes for each number of pairs of genes is definite and precise. But an actual sample of a population resulting from a particular number of pairs of genes does not bear so definite and precise a relation to its theoretical population, because of sampling effects. When, then, it is compared with theoretical curves, as the ideal sample was compared, its end classes rarely correspond with their theoretical position. As a consequence, the number of classes included in the sample may be larger or smaller than in a theoretically ideal sample. A curve might be fitted to the observations, but this labor can be avoided and practical purposes served by the expedient of calculating a lower and an upper limit of selection, as is done later in this paper. Since the actual number of pairs of genes is not known in advance and may never be known, great accuracy is not needed. All that can be done is to make estimates that cover all reasonable possibilities.

The relation of an actual sample to the theoretical population can be determined from the terms of the expanded binomial, if the number of pairs of genes is not too large. When the number becomes too large, resort may be made to a table of the probability integral. Such a table shows that .9544 of all individuals occur within the limits of $\pm 2\sigma$ and that .9974 occur within the limits of $\pm 3\sigma$. The proportion occurring between $\pm 2\sigma$ and $\pm 3\sigma$ is .0430 which is .0215 on each side of the distribution. The proportion of the population outside $\pm 3\sigma$ is .0025 or .0013 at either end. When only thirteen individuals in ten thousand occur beyond $+3\sigma$, and correspondingly at the other end, it is evident that $+3\sigma$ marks the beginning of one area and -3σ of a second area, no representatives of which are likely to be included in a sample of this size or less. But if either end of a sample should by chance lie outside $\pm 3\sigma$, and if the estimate of the limits of selection be based upon the ends at this point, the only effect would be to make the estimate a little too large or, in the other direction, a little too small.

From the distribution of the normal curve, it is evident that the extreme classes of an actual sample of the size commonly obtained in biological work are likely to fall between $\pm 2\sigma$ and $\pm 3\sigma$ of the normal curve. If, then, the ends of the actual sample are made to correspond with each of these two points, upper and lower estimates of the range of the theoretical curve for any number of pairs of genes in terms of the units of measurements of the actual sample may be obtained. The ends of this theoretical range set the limits of selection for the number of pairs of genes concerned. As sigma is easily calculated for any number of pairs of heterozygous genes of equal frequency and equal effect, being the square root of half the number of pairs of genes, and as the number of genetic classes is known from the number of pairs of genes, the amount of change to be expected is easily computed.

The number and per cent of the genetic classes between -2σ and $+2\sigma$, and between -3σ and $+3\sigma$, for various numbers of pairs of genes—selected be-

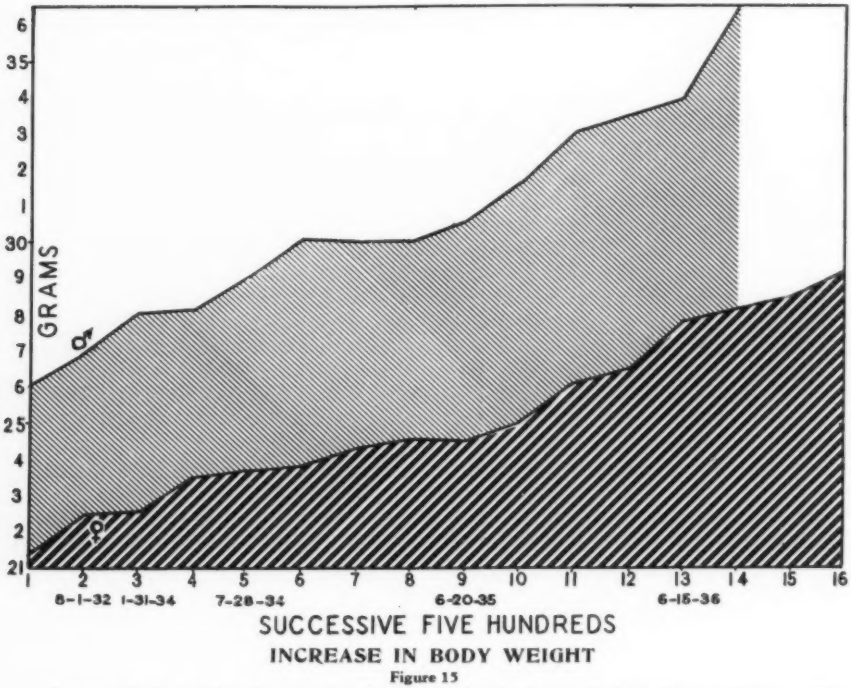


Figure 15

Average body weight of successive five hundreds of mice studied in this experiment. The number of generations reported by the graph is between twelve and sixteen. During this period of gentoypic (progeny) selection the rate of gain has varied somewhat, but it is not yet slackening. The chart summarizes observations which indicate that mice can be bred as large—or larger than rats. The birth-dates of certain mice are given at the bottom of the chart: 501—Aug. 1, 1932; 1001—Jan. 31, 1934; 2001—July 28, 1934; 4001—June 20, 1935; 6001—July 15, 1936.

cause sigma is a whole number—and beginning with 32 pairs of genes—are shown in Table 1. The application of the proportions obtained in Table 1 is made in Table 2.

In making the computations, the results of which are shown in Table 2, it has been assumed that the weights (Figure 16) of the early descendants of the foundation mice are substantially equivalent to a random sample of one thousand individuals drawn from the same population as the foundation mice. This assumption is sufficiently close to the truth for present purposes as is shown by statistics on weight of other mice which are given below. However, because selection was begun without collecting statistics on a random sample of the foundation stock, the maximum weights shown in Table 2 were computed by taking the center of distribution at 25 grams, the

TABLE 1

Pairs of Genes	Sigma	Number of Genetic Classes	Genetic Classes between: -2σ and $+2\sigma$ Number	Per cent	-3σ and $+3\sigma$ Number	Per cent
32	± 4	65	16	25	24	37
50	± 5	101	20	20	30	30
200	± 10	401	40	10	60	15
5,000	± 50	10,001	200	2	300	3
20,000	±100	40,001	400	1	600	1.5

range at 12 grams and the two ends of the range at 19 grams and 31 grams.

To illustrate the method of computing maximum weight, suppose that 32 pairs of heterozygous genes influence weight. The two ends of the range, 19 gr. and 31 gr. (Fig. 16), are placed at—2σ and $+2\sigma$, respectively, of the normal curve. There are, then, 65 genetic classes (Table 1) of which 16 occur between -2σ and $+2\sigma$. The 16 genetic classes are, in round numbers, one-fourth of all genetic classes, and since the 16 genetic classes are equal to 12 grams, the 65 genetic classes would be four and one-sixteenth times twelve, or 48.75 grams. As half the range is on either side of the mean, the maximum weight of male mice is 25 + 24.4, or 49.4 grams.

This table of estimates of the maximum weight to which mice can be bred by the accumulation of genes favoring increased weight must be considered with due regard to its limitations, both of method and of the complications introduced by the known variations in behavior of genes. Notwithstanding all these difficulties, the table shows that the possibilities for producing change through the accumulation of favorable genes may be large. How large depends upon the number of different loci represented by unlike alleles which are judged to exist in the foundation animals.

Selection for Increased Weight

The report on selection for increased weight in mice, which is made at this time, is in the nature of a progress report as the work is being continued. The foundation mice used in the experiments were albinos of no particular distinction, obtained from a commercial breeder. Four males and eight females were received on April 3, 1930, and twelve females on May 14, 1930. On January 27, 1931, four males and eight females were added. Since then, no additions have been made. Some of the foundation mice had no children, while others had children but no grandchildren. The consequence is that all mice used as breeders which had offspring born after January 29, 1934, — the date of birth of male 1000 — are descended from five of the foundation males and eleven of the foundation females. It follows, then, that no more than these sixteen mice are represented in the ancestry of later generations.

In the early stages of the experiment, certain difficulties were encountered which were solved as the experiment proceeded. Thus weights were taken of every mouse, but as we did not know the best age for weighing mice, weights were taken at various ages in its early stages. Enough were taken at the age finally established as best suited to the needs of this experiment to provide a basis for reference and comparison. However, the basis may be influenced to some extent by the selection for increased weight which began before all of these weights were taken (Figure 16). The males averaged 26.0 grams, the females 21.3, which is greater than that of the dilute chocolates reported by Green[7,8] by some twenty-five per cent and nearly forty per cent greater than that of albinos reported by Robertson.[12,13] Dr. Alfred Marshak has kindly supplied the sixty-day weights of his *B* strain.[10] The males of this strain averaged 21.9 grams and the females 18.4 grams. For further comparison, and to learn why the mice of the early generations of the experiment were so much heavier than the others, inbred agoutis, not selected for increased weight, descended from foundation mice received from Dr. Lionel Strong and inbred by

TABLE 2

Pairs of Genes	Maximum Weight ±2 sigma	±3 sigma	Approximate Number of Individuals Required to Obtain the Two Extremes
2		31.0*	16
5		31.0*	1024
10		33.8*	10×10^5
20		37.9*	11×10^{11}
32	49.4	41.3	18×10^{18}
50	55.3	45.2	13×10^{29}
200	85.2	65.1	26×10^{119}
5000	325.0	225.0	20×10^{2000}
20000	625.0	425.0	16×10^{12000}

*Computed from the expanded binomial, not from $\pm 3\sigma$ of the normal curve.

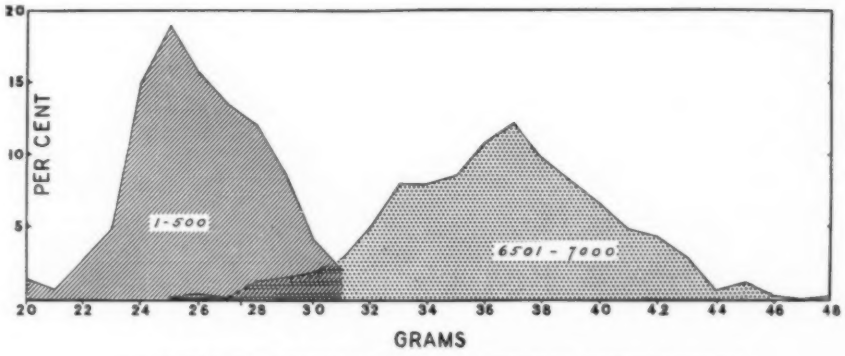
him for twenty-four generations, have been weighed during the past year. The males average 24.3 grams and the females 21.8 grams. The mice of the Strong strain, like the early mice of the experiment, are considerably heavier than the others, which indicates that the foundation mice probably were not substantially different genetically from the Green, Robertson and Marshak mice, but owe their weight to methods of management.

As the chief object of this experiment is the production of as great an increase in body weight of mice as possible through the agency of selection, it has been allowed to develop freely. Matings are made without regard to relationship or age. Consequently, there is some over-lapping of generations. The working program is as follows:

Once every week three males, not previously mated, are mated, each to several females, usually five. These mice are usually the largest which are available at the moment, but when the weights of the members of a family of full sibs are uniformly near the top, its members are given preference over members of other families. Mice weighed during the preceding week, other things being equal, are given preference over older mice. The males are retired from service as soon as their mates are pregnant, and remain out of service until their offspring are old enough to be separated from their mothers. A male whose offspring are conspicuously large to the eye at this time, is immediately re-mated to the same females. Males whose offspring are not conspicuous because of size remain out of service until their offspring are weighed. Few return to the breeding pens, the remainder being discarded. Females which are mothers for the first time are not re-mated immediately, unless they have children of exceptional size at one month of age. In this event—space permitting—they are mated to males that have demonstrated their ability in siring large children. The others are held until their children are weighed. Then they are mostly discarded, but some whose children pass the weight standard are re-mated. Able parents of either sex are continued in service until they are no longer useful. The essential element in this experiment is, therefore, genotypic selection to which the phenotypic selection of young animals is merely a necessary preliminary. Each pregnant female is placed in an individual cage where the young are born and where they remain until one month of age. Then the sexes are separated, members of two—sometimes more—litters being placed in the same cage, when numbers and dates of birth permit. At this time each mouse is given an identifying number in consecutive order and earmarked. They are weighed one month later, and this weight is used as the basis of selective mating and as a measure of results.

The litters are never reduced in size but all mice born are allowed to live, except an occasional mouse suffering severely from diarrhoea at ear-marking time, but such mice are now very rare. For a time, until the cages were set on rails, many deaths were due to a contagious form of diarrhoea whose etiology was never determined. Now, the only deaths between marking and weighing are from occasional weak individuals that reach one month of age but do not live until weighing time. These deaths are never the product of human intervention and, so far as can be determined, are rarely due to cage mates.

The figures which are being reported at this time are given in terms of the average weight of mice at intervals of five hundred numbers. Five hundred numbers do not necessarily mean that five hundred mice are weighed, because of an occasional death and an occasional loss from some mishap in the laboratory. Since the mice are numbered consecutively in order of birth, presenting the results of this experiment in terms of weight of the mice at intervals of successive five hundreds corresponds, therefore, to the continued addition of new generations, exactly as would happen if the weight of every human being on his twenty-first birthday had been recorded for the last thousand years. And, as



ONLY SLIGHT OVERLAPPING IN WEIGHT DISTRIBUTION

Figure 16

The weight of the first five hundred male mice averaged ten grams less than the last five hundred, and the average of the last five hundred was several grams greater than the heaviest mouse among the first five hundred. Furthermore the variability in the later generations is greater than in the earlier, which suggests that the limit of selection has not yet been approached in the 12 - 16 generations of the experiment to date.

with human beings, the number of generations in the ancestry of mice born on the same day is not exactly the same. Thus, a count of filial generations in the direct (father to son, or mother to daughter) line of descent among five males and five females, not brothers nor sisters, nearest male 6001 and female 7001, gives sixteen generations as the greatest number and twelve as the least number of generations from this point in the experiment to the foundation mice.

The number of mice reared to two months of age has been changed from time to time. Thus, male 1001 was born on January 31, 1934, nearly four years after the arrival of the foundation mice, which is at the rate, for both sexes, of five hundred young mice per year. During the following year the number of young mice was increased to the present number of four thousand per year. On this account the dates of birth of certain mice are given on the graph (Figure 15) to establish their general relationship with the numbers.

The Results of Selection

The trend of the results of the form of selective breeding used in this experiment is unmistakable (Figures 15 and 16). The line of averages is a line of ascent, though with periods of hesitation. The average gain for the males is 1.48 grams per thousand mice recorded and for the females, .99 per thousand. The rate of increase in average weight is 1.2 grams per thousand mice recorded, or .6 of a gram per generation. The average weight of males in the first five hundred numbers is 26.0 grams. The last five hundred males average 36.4 grams, an increase of forty per cent. Female weights are 21.3 grams and 29.3 grams, an increase of nearly thirty-seven per cent. Moreover, as shown by Figure 16, the present average weight exceeds the maximum weight of mice in the early generations by several grams.

The heaviest mouse at two months of age to date is number 6881, a male, weighing 48.1 grams. According to Table 2, the heaviest male expected when there are 50 pairs of genes, and when it is assumed that the extreme weight classes of the sample of the unselected population correspond with $\pm 3\sigma$ of the normal curve, is 45 grams. For the purposes of the following estimates, this weight may be regarded as the genetic equivalent of the 48.1 gram male. To obtain one male of this weight — or its equivalent in a female — without selective breeding, by segregation in an F_2

generation of 50 pairs of heterozygous genes, requires on the average the examination of 126×10^{28} mice.

This number of mice is too large for easy comprehension. A better comprehension of its magnitude may be had by converting it into weight for comparison with some familiar object. If there are 19 mice to the pound (23.9 grams each, which is close to the average of the early males and females shown in Figure 15), 126×10^{28} mice would weight 3336×10^{22} tons. The weight of the earth is estimated to be 6×10^{21} tons. Thus the total weight of the mice that must be examined to find that one mouse in 126×10^{28} mice is 5560* times the weight of the earth.

Using weight at two months of age as the basis of mating and of records has not resulted in precocious attainment of final weight, as figures given later in this paragraph show. At the beginning of the experiment, the two months' weight was approximately two-thirds the adult weight of males or females which were carried to maturity without being allowed to mate. But the practice of retaining unmated animals has been discontinued because it absorbs so much of the working capacity of the laboratory. The breeding females are, however, mostly weighed on the day they are discarded. Sixty-nine females between the ages of 160 days and 189 days were weighed between January 1, 1937, and this writing. Their average weight at two months was 31.9 grams and at the average age of 170.6 days, 44.6 grams. The mice continue to increase in weight beyond this age because twelve females weighed between December 4, 1936, and this writing, and averaging 246.3 days of age, weighed 51.9 grams. The average weight of these twelve, at two months, was 33.1 grams.

One of the interesting by-products of the experiment is the occurrence of mice which are very large at one month of age. Occasionally, some of the largest are weighed. The maximum weight at this age is 31.2 grams for males and 29.3 grams for females.

Discussion

The present status of this experiment permits of no final conclusions. Nevertheless, certain statements on the nature and number of genes concerned may be made at this time.

1. The weight of the heaviest mice indicates (Table 2) the existence of at least 32 pairs of weight genes.
2. An examination of our files shows that regression is a characteristic feature of the matings of the heaviest mice of the moment, but regression is not expected from non-dominant genes.
3. The proportion of individuals in the genetic class containing all phenotypic dominants is so high (.3 per cent for 20 pairs of dominant genes) that the current large mice must represent the accumulation of many more than 20 pairs of dominant genes.
4. The accumulation of recessives is said to result in loss of vigor. If this is true of the recessives of weight genes, increased weight can scarcely be due to accumulated recessives, as the large mice are not less vigorous than the small ones. Moreover, if increased weight is due to recessives, some matings of the heaviest mice of the moment should show no regression.
5. Reports on crosses between large and small races of mice, Green,[7,8] Castle et al.,[4,5] in which F_1 is intermediate in weight or nearer the larger parent, suggest that small weights are not due to accumulated inhibitors.
6. As small mice in general are not less vigorous than large ones, they can scarcely be due to the accumulation of recessives (cf 4).

It has been shown that the increased weight of the mice of this experiment can be explained in terms of the multiple factor hypothesis. However, it is well to remember that the multiple factor hypothesis carries certain implications, one of which may be mentioned here because of its potential consequences. The increase in weight of the heaviest mice of today over the heaviest mice at the beginning of the experiment has been referred to the accumulation of plus genes, which were already present in the sixteen foundation mice but which were distributed in such a way that their presence was not manifest to the eye nor to the scale. But what of the allels of each

* Sufficient places were carried in the computations to obtain arithmetical accuracy in this figure.

of these plus genes? Would their accumulation by selection result in a decrease in weight of the same amount as the increase, as might be inferred from the theoretical extent of the range on either side of the mean? If so, it should be possible to breed males weighing only three grams at two months of age and females in proportion.

While the multiple factor hypothesis of size inheritance is quite generally accepted by geneticists and is to be regarded with favor in explaining the results of this experiment, two other ways of explaining it may be mentioned.

First: The increase in maximum size of the mice may be explained on the assumption that several gene mutations favoring increased weight occurred during the course of the experiment. But these gene mutations differ in several respects from the gene mutations most studied. A gene mutation is a change in a definite but restricted area of a chromosome,—a locus. They are erratic and unpredictable events, for a gene mutation may affect any character of the organism in any direction and to almost any degree. The rate at which they occur has not been determined exactly, but it is relatively low. In discussing this point, Fisher,[6] said, "The rate of individual mutations in Drosophila is certainly seldom greater than one in 100,000 individuals." Recent work indicates that gene mutations occur more frequently than has been supposed (H. H. Plough, in a letter). Nevertheless, they are not common events in relation to the number of individuals used in this experiment.

Now the increase in weight, due to each of the assumed plus* gene mutations whose combined effect has resulted in a slow, gradual increase in the maximum weight of the mice of this experiment, must be small because the increase in maximum weight has been about a gram per generation. If each such increase is taken to mark the occurrence of an additional gene mutation, the mutation rate is one in a thousand. This method of estimating the rate of gene mutation is open to serious objection, but however the estimate is made, the conclusion appears inevitable that a remarkably high rate is required in order to explain the increase in maximum weight by mutations. Moreover, if they affect other characteristics of the mice, as many mutations do, the changes have been so inconspicuous that they have escaped notice. Thus these assumed gene mutations are not the rare, erratic and unpredictable events so well known, but events which act as if they were obedient to the will of the breeder.

Second: It is necessary to consider now the possibility that selection may act on the germ cells, particularly on the chromosomes of the germ cells, in some way which is not included in present conceptions of genes and gene mutations. Consideration of this possibility is necessary because a growing body of evidence indicates that gene mutations are injuries to local areas—loci—of the chromosomes. As the chromosomes are linear bodies, injuries are necessarily arranged in a linear sequence, but this need not mean that the chromosomes are structures like a chain or string of beads, or that the genes are normal units of inheritance. Since the concept of the gene as the normal unit of inheritance developed from a study of gene mutations, the evidence that mutations are injuries to chromosomes challenges this concept of the gene. For example, Jennings,[9] asks the following questions, — questions which a few years ago would have remained unasked: "Are all gene mutations that occur under the action of radiation the result of chromosome breakage or injury? And further are all gene mutations of this type?"

After discussing the effects of gene mutations upon the organism in which they occur, he goes on to say:

While it is thus clear that most gene mu-

*Mutations without effect on weight or with a minus effect would pass unnoticed if they occurred during the course of this experiment because selection was exclusively in the plus direction, unless they had a conspicuous effect on some other character of the mouse.

tations are not of such a nature as to result in progressive evolution, it is held probable by most students of the matter that among the great number of injurious mutations there may occur a few that are advantageous. It is these that would form the basis for evolutionary progress.

On the other hand, it may turn out that gene mutations of the sort thus far observed are not the material of progressive evolution. It may be that we have not yet recognized the actual steps in progressive evolution, and that when these come clearly into view, it will be found that they are not the result of action of destructive agents, nor connected with injuries to the genetic system, but rather bear a resemblance to the changes of growth. These questions must be reserved for the future.

If Jennings is correct in supposing that the materials of progressive evolution may bear a resemblance to the changes of growth, is it not possible that the effects of selection on a character, such as size, may involve some process other than the accumulation of genes new or old? The answer to this question also lies in the future, but the question itself can no longer be disregarded.

The results of this experiment in genotypic selection for increased weight raise several other questions which again must be reserved for the future. However, a few brief comments may be made now.

1. Genotypic selection is a very different matter from phenotypic selection (cf Pearl,[11]). Consistent application of this principle may very well lead to continued change, whereas phenotypic selection quickly reaches the limit which appears so frequently in reports on selection experiments. It is possible — though this experiment does not settle the question — that the increase in the weight of the mice of this experiment could not have been secured by phenotypic selection alone.

2. The doctrine of evolution through natural selection is a derivative of those forms of selection practiced by man. Natural selection may seem to be wholly phenotypic, containing no element of genotypic selection, but this view overlooks the fact that a larger proportion of offspring of some matings survive than the offspring of other matings, just as in any selection experiment based on the progeny test (genotypic selection), a larger proportion of offspring of some matings gain the breeding pens than of other matings. Natural selection and mating are very likely less stringent than artificial selection and mating, but time and numbers give nature an advantage wholly lacking in any human experiment. Natural selection may, therefore, promote changes in species through the accumulation of small inherited advantages in the manner which Darwin proposed.

3. The possibilities for the improvement of farm animals by genotypic selection is very great, much greater, indeed, than is realized by breeders.

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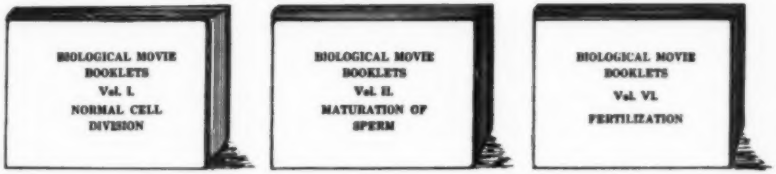

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